

The repeatability of stem exclusion during even-aged development of bigtooth aspen dominated forests

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Forest development following major disturbance is thought to follow a fairly repeatable temporal pattern. An initial cohort of trees establishes relatively rapidly (stand initiation), new establishment is precluded for an extended period (stem exclusion), and finally, new individuals again begin to establish, creating new age-classes in the forest understory (understory reinitiation), eventually leading to an uneven-aged condition. The current study was designed to assess the generality of this developmental pattern at the landscape level and gain insight into the possible mechanisms controlling stem exclusion and understory reinitiation in even-aged forests. Research was conducted within two bigtooth aspen (*Populus grandidentata* Michx.) dominated landscapes in northern Lower Michigan having similar physical site characteristics, overstory compositions, and disturbance histories. The objectives for the study included (i) assessing the repeatability of development patterns within and between the two landscapes and (ii) exploring relationships between the timing of understory reinitiation and overstory growth characteristics and seed availability. Stem analysis was used to reconstruct establishment and growth histories of surviving stems in mature forest on replicate plots within each landscape. The age distributions of surviving individuals of all tree species in both forests reflected a developmental pattern characterized by rapid initial cohort establishment lasting 5–15 years, stem exclusion lasting 25–35 years, and understory reinitiation. The duration and timing of the developmental stages on the replicate plots were similar both within and between the two landscapes. There were, however, a small number of plots in landscape 2 that had substantially reduced stem exclusion lengths, relative to the remaining plots in both forests. Variation in the timing of understory reinitiation in landscape 2 was related to characteristics of remnant eastern white pine (*Pinus strobus* L.) seed trees. The stem exclusion period was shorter, or almost nonexistent, on plots close to several large seed trees because of early, low-frequency establishment of white pine in the understory. Substantial increases in the frequency of understory establishment on all plots in landscape 2, as well as all new understory establishment on plots in landscape 1, were often associated with radial growth increases in overstory stems. The radial growth increases presumably reflected an increase in resource availability, possibly occurring in response to a concentrated wave of natural thinning within the bigtooth aspen dominated overstory. These results suggest that the timing of understory reinitiation may have been influenced by variation in seed availability interacting with changes in resource availability in the forest understory. A limited amount of new establishment occurred relatively early in forest development on plots that experienced abundant early seed rain, yet the bulk of new establishment occurred only after an increase in resource availability in the understory. The general patterns of forest development described in this study were similar both within and between landscapes. Similar descriptive studies are needed to address the repeatability of development patterns at the landscape level within other forest types. Additionally, experimental studies are needed to unequivocally identify the mechanisms controlling stem exclusion and understory reinitiation in even-aged forests.

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On considère généralement que l'évolution des forêts après une perturbation majeure suit un patron temporel assez facilement reproductible. Un groupe initial d'arbres s'établit assez rapidement, le recrutement de nouvelles tiges est exclu pour une période prolongée, et, finalement, l'établissement de nouveaux individus redevient possible, créant de nouvelles classes d'âge en sous-étage, aboutissant ainsi éventuellement à une forêt âgée inéquienne. L'étude présentée a été conçue pour vérifier la possibilité de généraliser ce patron de développement à l'échelle de l'unité de paysage et d'approfondir la compréhension des mécanismes régissant l'exclusion du recrutement et la réinstallation du sous-étage dans les forêts équienues. Les travaux de recherche ont été réalisés dans deux unités de paysage dominées par le peuplier à grandes dents (*Populus grandidentata* Michx.), dans la partie nord du Michigan inférieur où les caractéristiques physiques de station, la composition du couvert et l'historique des perturbations étaient semblables. Les objectifs de l'étude étaient (i) évaluer la reproductibilité des patrons de développement à l'intérieur et entre les deux unités de paysage et (ii) explorer les relations entre le moment où débute la réinstallation du sous-étage et les conditions de croissance du couvert et la disponibilité des semences. L'analyse de tiges a été utilisée afin de reconstruire l'historique de l'établissement et de la croissance des tiges ayant survécu jusqu'à maturité sur les répliqués à l'intérieur de chacune des unités de paysage. La distribution des âges des individus ayant survécu, pour toutes les espèces et dans les deux forêts, reflète un patron de développement caractérisé par un établissement rapide s'étendant sur 5 à 15 ans, par une phase d'exclusion d'une durée de 25 à 35 ans, et par une réinstallation du sous-étage. La durée de même que le moment où surviennent les étapes de développement sur les répliqués étaient semblables, à la fois entre et à l'intérieur des deux unités de paysage. On a toutefois observé un petit nombre de parcelles dans l'unité 2 où la phase d'exclusion était substantiellement réduite, par rapport aux autres parcelles dans les deux forêts. Une variation dans la période d'occurrence de la réinstallation du sous-étage dans l'unité 2 de paysage était liée aux caractéristiques des arbres rémanents de pin blanc (*Pinus strobus* L.). La période d'exclusion était ainsi courte ou presque absente sur les parcelles situées à proximité de plusieurs semenciers de fortes dimensions à cause d'un établissement faible et hâtif du pin blanc en sous-étage. Des augmentations importantes dans la fréquence d'établissement en sous-étage sur toutes

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les parcelles de l'unité 2, de même que l'ensemble de l'établissement en sous-étage dans l'unité 1, coïncidaient souvent avec une augmentation de la croissance radiale chez les arbres du couvert. Cette augmentation de la croissance radiale traduit probablement une augmentation de la disponibilité des ressources, possiblement survenue à la suite d'une période importante d'éclaircie naturelle à l'intérieur du couvert dominé par le peuplier à grandes dents. Ces résultats suggèrent que la période de réinstallation du sous-étage a pu être influencée par des variations dans la disponibilité des semences en interaction avec des modifications dans la disponibilité des ressources en sous-étage. Un établissement réduit est survenu relativement tôt sur les parcelles où la chute de semences était abondante en jeune âge, mais la majorité de l'établissement est uniquement survenue après une augmentation de la disponibilité des ressources en sous-étage. Les patrons généraux de développement des forêts décrits dans cette étude étaient similaires à la fois entre et à l'intérieur des unités de paysage. D'autres études semblables demeurent nécessaires pour évaluer la reproductibilité des patrons à l'échelle de l'unité de paysage dans d'autres types de couvert. De plus, des études expérimentales sont nécessaires afin de cerner sans équivoque les mécanismes régissant l'exclusion des tiges et la réinstallation du sous-étage dans les forêts équiennes.

[Traduit par la rédaction]

Introduction

Even-aged forest development has received considerable attention over the last several decades (for example, see Bormann and Likens 1979; Oliver 1980, 1981; Peet and Christensen 1987). This interest can be attributed in part to the prevalence of an even-aged structure in managed forest landscapes, but also to the realization that large-scale natural disturbances have created single-age-class forests in many regions (see examples in Lorimer 1980; Oliver 1981). The development of even-aged forests is thought to follow a fairly repeatable temporal pattern (Oliver 1981; Peet 1981; and others cited in Peet and Christensen 1987). An initial post-disturbance cohort of trees becomes established during a relatively short period (stand initiation sensu Oliver 1981). A second period follows during which few or no new individuals become established (stem exclusion). Following stem exclusion, individuals of overstory tree species again begin to establish successfully, creating new age-classes in the forest understory (understory reinitiation).

Many silvicultural studies of even-aged forest development have explored growth patterns within the initial post-disturbance cohort of trees (Cayford 1957; Oliver 1978; Wierman and Oliver 1979; Hibbs 1983; Guldin and Lorimer 1985; Kelty 1986; Larson 1986; Clatterbuck and Hodges 1988; Hix and Lorimer 1990, 1991; Palik and Pregitzer 1992a). Less attention has been given to characterizing and understanding, from a mechanistic perspective, the stem exclusion and understory reinitiation phases of even-aged forest development. While one or both of these developmental stages have been documented in a wide variety of forest types (Bloomberg 1950; Sprugel 1976; Oliver 1978; Christensen and Peet 1981; Peet 1981; Oliver et al. 1985; Roberts and Richardson 1985; Harcombe 1986; Sharik et al. 1989; Abrams and Nowacki 1992; Segura and Snook 1992), few studies have been designed to assess the repeatability of stand development patterns within and among landscapes characterized by similar physical site characteristics, species compositions, and disturbance histories (for a notable exception see Sprugel 1976). The need for assessing the generality of developmental patterns is demonstrated by the fact that some forests initiating after major disturbance have actually been found to lack a stem exclusion period (Peet 1981; Carleton 1982; Roberts and Richardson 1985; Palik and Pregitzer 1991).

There is also a lack of consensus regarding the mechanisms that control stem exclusion and understory reinitiation in even-aged forests. Some studies suggest that stem exclusion may simply reflect an initial lack of local seed sources early in forest development, while understory reinitiation reflects the reproductive maturation of a post-disturbance cohort of trees

(Day 1972; Carleton 1982; Robberts and Richardson 1985; Sharik et al. 1989). In contrast, resource-based theories of forest development (Oliver 1981; Peet and Christensen 1987) suggest that stem exclusion begins after the initial cohort of trees attains full site occupancy, thereby limiting successful establishment through competition, despite the presence of a local seed source. Understory reinitiation is thought to begin only when resources become less limiting. Various mechanisms have been proposed to account for this increase in resource availability, including canopy gap formation following density-independent mortality of mature overstory individuals late in even-aged development (Sprugel 1976; Christensen and Peet 1981; Peet and Christensen 1987), crown differentiation within the even-aged overstory (Bormann and Likens 1979; Oliver et al. 1985; Oliver and Larson 1990), reductions in rates of root growth (Oliver and Larson 1990), and density-dependent mortality of suppressed individuals following a concentrated wave of natural thinning (Harcombe 1986; Oliver and Larson 1990; Palik and Pregitzer 1992b).

In this paper we report on a mensurative study designed to assess the generality of developmental patterns in even-aged forests at the landscape level and gain insight into possible mechanisms controlling stem exclusion and understory reinitiation. The study was conducted within two bigtooth aspen (*Populus grandidentata* Michx.) dominated landscapes in northern Lower Michigan, United States. Both landscapes are representative of aspen-dominated forests that occupy over 5×10^6 ha in the Great Lakes region (bigtooth and trembling aspen (*Populus tremuloides* Michx.) combined, Einspahr and Wyckoff 1990). Our initial objective was to reconstruct the establishment history of individuals from all tree species in these forests and assess the repeatability of development patterns within and between the two landscapes. Our second objective was to explore relationships between the timing of understory reinitiation (or conversely, the length of stem exclusion) and overstory growth characteristics and seed availability. Our working hypothesis associated with this objective was that understory reinitiation is controlled by an increase in resource availability associated with natural thinning within the bigtooth aspen overstory. Testable corollaries to this hypothesis were that (i) understory reinitiation would begin prior to the onset of mortality in mature, overstory dominants; (ii) understory reinitiation would be associated with increased radial growth in surviving overstory individuals, suggesting increased resource availability as a factor influencing survivorship in the understory; and (iii) the timing of understory reinitiation would be unrelated to characteristics of remnant seed trees (proximity, number, size) when they were present.

Study locations

Research was conducted within the Huron–Manistee National Forest (Huron) in northeastern Lower Michigan (44°15' to 45°00'N, 83°15' to 84°45'W) and the University of Michigan Biological Station (UMBS) in the extreme northwestern portion of Lower Michigan (45°40'N, 84°40'W). The two study areas are separated by approximately 150 km.

Surficial geology of both study areas consists of deep outwash sands overlying till deposits (Cooper 1981; Padley 1989). Soils throughout the majority of both study areas are classified as Entic Haplorthods (Cooper 1981; Lapin 1990; USDA Soil Conservation Service 1991; Michigan State University, Forestry Department data file). Both study areas are internally homogeneous with respect to physiographic, edaphic, and compositional (bigtooth aspen dominated) characteristics (Lapin 1990; Michigan State University, Forestry Department data file).

Prior to settlement, the Huron landscape was dominated by red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), and eastern white pine (*Pinus strobus* L.). The UMBS landscape was dominated by eastern hemlock (*Tsuga canadensis* (L.) Carr.), American beech (*Fagus grandifolia* Ehrh.), white pine, and red pine. Minor species common to both presettlement forests included bigtooth aspen, red maple (*Acer rubrum* L.), and northern red oak (*Quercus rubra* L.). A more detailed description of the presettlement forests of both areas can be found in Palik and Pregitzer (1992c).

The regions containing the study areas were deforested in the late 19th to early 20th centuries (Gleason 1923; Kilburn 1957, 1960a, 1960b; Benninghoff and Cramer 1963; Whitney 1987). Slash-fueled wildfires swept over these landscapes in the years following logging, eliminating advanced reproduction and most remnant overstory individuals of the dominant presettlement species (Kilburn 1957, 1960a, 1960b; Whitney 1987). Additionally, the fires promoted vigorous vegetative regeneration of aspen from rapidly spreading clonal root systems (Graham et al. 1963; Barnes 1966), which led to the development of strictly even-aged forests (Graham et al. 1963). The Huron study area did not contain any remnant individuals of the dominant presettlement species. In contrast, remnant white pine and red pine were scattered throughout the UMBS study area (Palik and Pregitzer 1992c).

Methods

Plot selection and vegetation sampling

Vegetation was sampled on a series of plots located within five stands in the Huron landscape and four stands at UMBS. Stands within each landscape belonged to similar ecological land classification units (following Barnes et al. 1982; Pregitzer and Barnes 1984). Selected stands met the following criteria: (i) minimum size of 1 ha; (ii) free from obvious disturbance since initiation; and (iii) 0–5% slopes. The distance between stands within each landscape ranged from 1 to 4.5 km. Four circular plots were located randomly within each stand. Plot size was 272 m² in the Huron forest and 475 m² at UMBS. A larger plot size was used at UMBS so that a similar number of overstory stems might be sampled as in the higher density Huron forest (see results). Plots were used as replicates in all statistical analyses. The species and diameter at breast height (DBH, breast height = 1.4 m) of all stems ≥ 2.5 cm DBH were recorded on each plot. Seedling (DBH < 2.5 cm) numbers were recorded in twelve 1-m² plots, spaced equidistantly at 3-m intervals along four opposing radii of each plot, beginning at the plot boundary. Seedlings were assigned to one of two height classes: <1.5 m or ≥ 1.5 m.

Destructive sampling

On each plot, one randomly selected bigtooth aspen, and all individuals ≥ 1.5 m tall of additional tree species, were destructively sampled to determine total heights, times of establishment, and rates of radial and height growth of selected overstory stems. For species other than bigtooth aspen, only the tallest ramets were sampled from multitemmed genets. For bigtooth aspen, one individual from the

dominant or codominant crown classes (most ramets were dominant or codominant) was randomly selected (rejecting ramets with internal decay) and destructively sampled on each plot. Sampling intensity for bigtooth aspen was much lower than for other species because little height variation was observed among dominant–codominant ramets within plots and little age variation was expected. The age distribution of sampled bigtooth aspen substantiated the latter expectation (see results).

On each plot, a subsample of individuals <1.5 m tall was sampled by stratifying on species and 0.5-m height classes. Stems <1.5 m tall were sampled primarily to determine the age range of these stems on each plot, particularly their maximum ages.

Stems were felled at 0.5 m or ground level (depending on size), and total heights were determined. Stem sections were cut at ground level from all larger individuals (generally those greater than 2.5 m in height). An additional section was removed at 1.4 m from all overstory individuals (DBH >10 cm) for use in radial growth analysis. Additionally, all bigtooth aspen stems were marked at 0.25-m intervals from the base to 2- and 1-m intervals thereafter. Marking continued to the 1-m multiple closest to the end of the dominant leader. Stem sections were cut at each measurement interval up to a 3 cm diameter top. All destructive sampling was completed during summer and fall of 1990.

Age determination

Small stems of deciduous tree species (generally those <2.5 m tall) were aged by counting the number of terminal bud scale scars preceding each height interval. Small stems of coniferous species (white pine and red pine) were aged by counting branch whorls. The accuracy of bud-scale and branch-whorl counts was checked by counting rings on basal and 0.25-m stem sections (typically the most difficult portion of the stem to age by these methods) on a subsample of stems under a dissecting microscope. Age determinations for the two methods seldom differed by more than ± 2 years and then only on individuals >2 cm basal diameter.

Basal stem sections of larger individuals were sanded to a smooth surface and wetted to aid ring examination. Ages of all sections were determined by counting the number of rings on at least two radii (typically a long and short axis on oblique-shaped stems) under a dissecting microscope. The oldest age of each section was recorded when the counts differed. Precision of ring counting was assessed by periodically recounting 20% of the stem sections from lots of 15–25 sections each. Recounts seldom differed by more than 1 year. Faint annual rings made accurate ageing of paper birch (*Betula papyrifera* Marsh.) impossible. All genets of this species were apparently of vegetative-origin (all multitemmed) and were probably of equivalent age as the sampled bigtooth aspen. Further, paper birch was not an important component on any of the sample plots (see results). American beech, white ash (*Fraxinus americana* L.), and balsam fir (*Abies balsamea* L.) were also rare in the sample plots (see results) and were excluded from analysis.

Terminal-bud-scale counts, branch-whorl counts, and ages of basal stem sections were used to determine time of establishment of all sampled stems. Time of plot initiation (years before sampling) was based on the mean age of all individuals that established within the first 10 years of plot development. Time of understory reinitiation was defined as the plot age (years after plot initiation) after which at least two new individuals established every 5 years for at least a 20-year period, with establishment being defined as survival to the time of sampling.

We caution that there are two potential minor sources of error associated with our estimation of stem exclusion lengths and timing of understory reinitiation. First, probability of mortality is a positive function of stem age. Therefore, older suppressed stems that established in the understory either at the end of initial cohort establishment or at the beginning of understory reinitiation may have died prior to sampling. This source of error would have the effect of overestimating stem exclusion lengths. Second, suppressed individuals that were actually sampled may have been several years older than they

appeared if they had dropped rings near their stem bases, as suppressed stems sometimes do (Larson 1956; Bormann 1965). This error would have the effect of either (i) underestimating stem exclusion lengths, if suppressed stems that established near the end of the initial cohort establishment period were underaged, or (ii) overestimating stem exclusion lengths, if suppressed stems that established near the beginning of understory reinitiation were underaged.

Radial and height growth analysis

Annual ring widths were measured along one randomly selected radius (rejecting decayed or injured areas) on the 1.4-m stem sections of overstory stems (DBH > 10 cm). Ring widths were measured to the nearest 0.1 mm using a dissecting microscope and ocular micrometer. For each stem, a standardized, dimensionless index of radial growth (ring-width index) was derived by dividing the mean ring width for the entire series into the actual ring width at each year. Ring-width series were not detrended, as is often done in dendroclimatological studies (Fritts 1976), since there was no a priori reason to remove age effects from the chronologies. Mean chronologies were developed by averaging the ring-width indices of several individuals on each plot. The ring-width standardization prevented fast-growing individuals from dominating the mean chronologies (Veblen et al. 1991). Individual tree chronologies were averaged in an attempt to dampen any nonsynchronous changes in radial growth patterns, while retaining any synchronous suppressions or increases that might reflect plot-level changes in resource availability during the course of forest development. The mean chronologies were developed using several red oak and red maple on each plot. We reasoned that subtle changes in resource availability within the matrix of bigtooth aspen ramets would be reflected best in the radial growth patterns of red oak and red maple, since these species are long-lived, relatively more understory tolerant than bigtooth aspen, and are known to respond to release with increased radial growth (Laidly 1990; Sander 1990; Walters and Yawney 1990). The number of individuals used to form the chronologies varied from 2 to 9 and depended on (i) the number of genets of these species on a plot, (ii) their age at 1.4 m (the goal was to extend chronologies as far back as possible without dropping individuals from the record), and (iii) their total heights (individuals <15 m in the Huron forest and <13 m in the UMBS forest were typically highly suppressed, so they were excluded from this analysis). Ring-width indices from sampled bigtooth aspen were not used in the chronologies. These ramets always grew relatively rapidly, as might be expected for stems of a very intolerant species (Laidly 1990) that were in dominant-codominant crown positions at maturity.

The terminal leaders and the additional stem sections from bigtooth aspen were prepared and aged as described previously. Section ages were used to reconstruct 5-year height increment curves for each stem. In some instances interpolation of stem height at a given plot age was necessary, since the stem sampling method controlled stem height but not age. In these cases, the shapes of age-height plots for the individuals involved were examined to ensure accurate determination of heights at the 5-year plot ages of interest.

White pine seed-source characteristics

The distance to and diameter of all remnant white pine seed trees were measured for each UMBS plot. Remnant trees were easily seen after leaf fall of bigtooth aspen. Potential remnant seed trees were restricted to a 130-m radius around the center of each plot. This was the distance to a sole remnant tree (within a 500-m radius) for a plot that contained a small amount of white pine regeneration. Large white pine could not be aged accurately because most individuals (from a subsample examined with an increment bore) had extensive internal stem rot. Instead, a remnant tree was defined as one ≥ 45 cm DBH. The 45 cm diameter limit was based on two lines of evidence. (i) Nonpublished age-diameter data for white pine (UMBS data file) indicated that trees <45 cm at the time of sampling in the current study would have predated bigtooth aspen by no more than 25 years. These individuals probably would have been too young to have reached reproductive maturity by the time of forest initiation (Wendel and Smith 1990). (ii) Sampling of white pine in the current study indicated

that the maximum diameter of stems establishing at or soon after stand initiation was <20 cm. Only one stand (four plots) contained any apparent remnant individuals with diameters greater than 20 cm but less than 45 cm.

Multiple regression was used to develop an exploratory model to examine the relationship between white pine seed-source characteristics and time of understory reinitiation for the species. The independent variables used in the model included (i) distance to the closest potential seed tree, (ii) mean distance to all potential seed trees, (iii) total number of potential seed trees, and (iv) mean basal area of all potential seed trees. The assumption associated with these variables was that plots in close proximity to several large seed trees would have had a greater probability of early white pine establishment because of greater seed rain early in forest development. Mean basal area was used not only as a measure of potential reproductive output, i.e., larger trees have more seeds, but also as a crude measure of timing of reproductive maturation. Larger diameter trees may not necessarily have been older than smaller diameter trees; however, they probably reached the size necessary for reproduction earlier than smaller trees. Ranked data were used in the regression analyses because of small sample sizes and poor structure of standardized residual plots. For all analyses, adjusted coefficients of multiple determination (Sokal and Rohlf 1981) are reported. There were too few plots with associated remnant red pine, and too little red pine regeneration in the understory of these plots, to conduct a similar regression analysis.

Results

Forest composition and structure

Present forest composition and structure of the Huron and UMBS study areas are summarized in Table 1. Bigtooth aspen was the dominant overstory species in both forests. Minor overstory species found in both forests included red oak, red maple, and paper birch. Red maple was virtually the only species regenerating in the Huron forest. White pine and red maple were both abundant as regeneration in the UMBS forest. Both overstory (DBH > 10 cm) basal area and density of the Huron forest were substantially higher than at UMBS. Sapling ($2.5 \leq \text{DBH} \leq 10$ cm) density was higher in the UMBS forest, while seedling densities were similar.

Population age structures

The age-height distributions for all sampled individuals on the Huron and UMBS plots are shown in Figs. 1 and 2. Only one bigtooth aspen ramet was sampled per plot; each plot contained an additional 15–35 bigtooth aspen ramets of similar age. In the Huron forest, an initial cohort of trees established within a 10-year period (Fig. 1), beginning 65–70 years prior to sampling (see plot ages in Table 2). All plots were characterized by an obvious period of stem exclusion during which few or no surviving individuals of any species established (Fig. 1). Mean (SD) time to understory reinitiation from the time of plot initiation was 34.5 (3.8) years. The near-synchronous timing of understory reinitiation on all plots is reflected in the low coefficient of variation for this event (11%). In only one instance was a stem <1.5 m tall older than the oldest understory stem ≥ 1.5 m tall, and then only by 1 year (plot H7, Fig. 1). Plot-level densities for stems establishing subsequent to understory reinitiation are shown in Table 2.

In the UMBS forest, most overstory individuals established within a 10-year period (Fig. 2), beginning 71–83 years prior to sampling (see plot ages in Table 2). Most plots were characterized by an obvious period of stem exclusion; however, in several plots (U1, U13–U16) this period was less obvious or nonexistent (Fig. 2). Mean (SD) time to understory

TABLE 1. Present forest composition and structure of the Huron and UMBS study areas

	Canopy ^a		Sapling (stems/ha) ^b	Seedling (stems/ha) ^c
	m ² /ha	Stems/ha		
Huron				
Bigtooth aspen	30.3 (2.1)	638 (48)	—	—
Red oak	5.5 (1.0)	166 (29)	13 (6)	3 625 (669)
Red maple	4.9 (0.6)	282 (28)	644 (89)	64 833 (6522)
Black oak	0.5 (0.2)	14 (7)	—	—
White oak	0.3 (0.2)	10 (5)	—	458 (260)
White ash	0.06 (0.06)	4 (4)	4 (4)	167 (97)
Paper birch	0.05 (0.05)	2 (2)	—	42 (42)
Black cherry	0.01 (0.01)	2 (2)	26 (9)	14 583 (3813)
Total	41.6 (2.0)	1117 (48)	686 (96)	83 708 (8205)
UMBS				
Bigtooth aspen	21.3 (1.2)	560 (41)	4 (4)	573 (225)
Red oak	2.5 (0.6)	67 (20)	82 (23)	4 740 (635)
Red maple	2.4 (0.4)	93 (23)	335 (69)	64 687 (8805)
Paper birch	0.9 (0.3)	46 (12)	54 (13)	—
Red pine	0.9 (0.4)	18 (10)	44 (20)	—
White pine	0.6 (0.2)	45 (15)	642 (127)	1 562 (569)
American beech	0.02 (0.02)	3 (3)	17 (7)	104 (71)
Balsam fir	—	—	3 (3)	—
Total	28.6 (1.5)	890 (44)	1180 (112)	71 666 (8777)

NOTE: Values are the means (SE) of 20 plots in the Huron forest and 16 at UMBS.

^aDBH > 10 cm.^b2.5 cm ≤ DBH ≤ 10 cm.^cDBH < 2.5 cm.

reinitiation was 24.9 (12.0) years. Understory reinitiation in the UMBS forest occurred significantly earlier than in the Huron forest (Student's *t*-test for unequal variances: *t* = -3.05, *df* = 17, *P* = 0.007), but variability for this event at UMBS was high, as reflected in the high coefficient of variation (48%). In the UMBS forest no stems <1.5 m tall were older than the oldest understory stem ≥1.5 m tall.

In some Huron plots, and most UMBS plots, there was an increase in establishment frequency beginning 30–40 years after plot initiation (Fig. 2). The timing of this increase was used to define a more conservative definition of understory reinitiation. Continuous understory establishment was defined as the number of years until at least one individual established every year, or two individuals established every 2 years, for at least a 10-year period. Determination of the timing of this event was not biased by incomplete subsampling of stems <1.5 m tall, since the maximum ages of these individuals never exceeded, and in fact rarely approached, the age of individuals ≥1.5 m tall that typically defined the start of continuous understory establishment (note that this period was defined exclusively by stems <1.5 m tall on plots H2, H6, and H15 because of a lack of stems ≥1.5 m tall; Table 2).

In the Huron forest, mean (SD) time to continuous understory establishment, from plot initiation, was 36.8 (3.5) years (CV = 9%). The mean (SE) difference between time to understory reinitiation and continuous establishment of -2.3 (0.5) years was low, but significantly different from zero (one-tailed Wilcoxon's signed-rank's test: *T*_s = 36, *N* = 20, *P* < 0.005). Mean (SD) time to continuous establishment in the UMBS forest was 33.8 (7.1) years (CV = 21%). The mean (SE) difference between time to initial understory reinitiation and continuous establishment of -8.8 (2.1) years was signif-

icantly different from zero (one-tailed Wilcoxon's signed-rank's test: *T*_s = 1, *N* = 16, *P* < 0.005). Non-normal residual distribution and heterogeneous variances prevented statistical comparison of time to continuous understory establishment between the Huron and UMBS forests. Failure to meet these assumptions was attributed to the presence of a single outlier among the UMBS plots (plot U15). In this plot, continuous establishment occurred much earlier than in the remaining 15 UMBS plots (13 years versus a mean (SD) of 35.1 (4.6) years). After excluding plot U15 from the analysis, variances were homogeneous (but residuals were still distributed non-normally), and the mean time to continuous understory establishment was not significantly different between the Huron and UMBS forests (Wilcoxon two-sample test: *U*_s = 181, *N* = 20 and 15, *P* > 0.20). Also, variability in the timing of continuous understory establishment in the remaining 15 plots at UMBS was low (CV = 13%).

Bigtooth aspen heights and height growth during understory reinitiation

In the Huron forest, mean (SD) height of the sampled bigtooth aspen at the time of understory reinitiation was 15.5 (2.1) m (63% of cumulative height at the time of stem sampling), while mean height at the time of continuous understory establishment was 16.5 (1.8) m (67% of cumulative height). The analogous heights in the UMBS forest were 8.4 (3.8) m (39% of cumulative height at the time of stem sampling) and 10.9 (2.9) m (50% of cumulative height), respectively. For the five UMBS plots with relatively early understory reinitiation times (U1, U13–16), mean (SD) height at the time of initial understory establishment was 3.6 (1.3) m (16% of cumulative height at the time of stem sampling), while mean height at

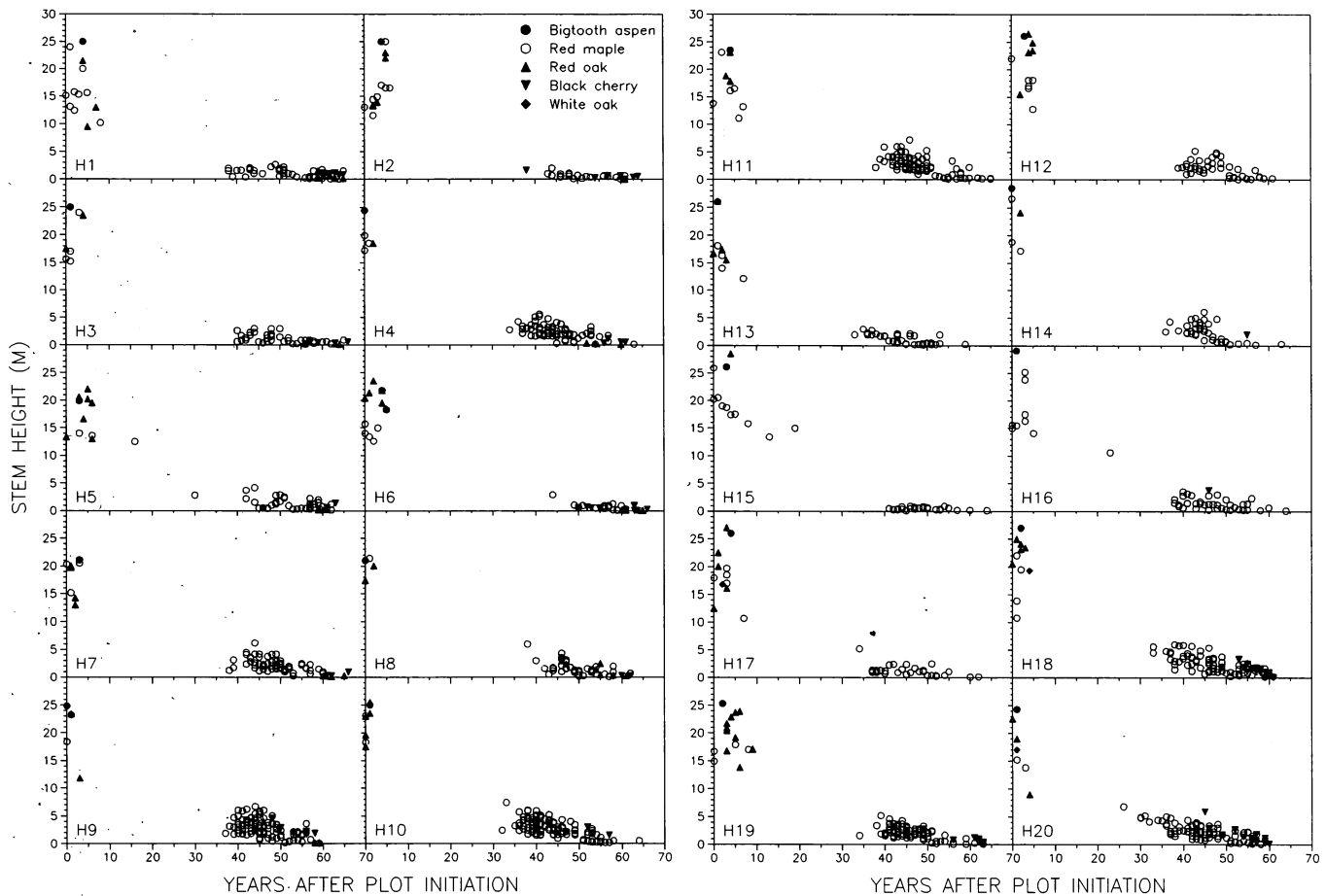


FIG. 1. Age-height distributions for all sampled stems on the 20 Huron plots. Individuals ≥ 1.5 m tall were completely sampled on each plot. Individuals < 1.5 m tall were subsampled. Note that each plot contained an additional 15–35 bigtooth aspen ramets of similar age as the sampled stem. Red oak and black oak (*Quercus velutina* Lam.) are combined under red oak.

the time of continuous understory establishment was 8.6 (4) m (38% of cumulative height). The sampled bigtooth aspen in the UMBS forest ranged from 15 to 35 years old at the time of understory reinitiation. In both forests, the sampled bigtooth aspen were, at most, 35 years old at the time of continuous understory establishment.

Height increment over time for the sampled bigtooth aspen is shown in Fig. 3. The overall trend in the Huron forest was one of early culmination in height increment, 20–25 years after forest initiation, and followed a large decline after this period. Both understory reinitiation and continuous understory establishment occurred subsequent to the decline. The height increment pattern of aspen in the UMBS forest shows an initial early decline followed by a secondary increase, 40–45 years after plot initiation, and a gradual decrease thereafter. The start of continuous understory establishment typically coincided with the secondary peak in height increment. Overall, height growth rates of bigtooth aspen at UMBS were low and only approached those of Huron bigtooth aspen early in forest development.

Patterns of radial growth and understory reinitiation

Ring-width chronologies for the Huron plots are shown in Fig. 4. The chronologies are missing for plots H17–H20 because the stem sections from these plots were inadvertently destroyed prior to measuring radial growth. The most obvious

and consistent features of the Huron chronologies were peaks in mean ring-width indices occurring 10–15 and 20–25 years after plot initiation (one or both peaks occurring in most plots, Fig. 4). Radial growth rates for the latter peak averaged 90% above the previous 5- to 7-year period and lasted 5–10 years. Subtler, and inconsistent, features of the Huron chronologies included fairly sharp decreases in mean ring-width indices, lasting 2–5 years, beginning 30–35 years (H2, H4, H10) and 40–45 years (H2, H3, H5, H6, H8, H16) after plot initiation. Growth rates during the decreases were 40–100% below both the previous and subsequent 5-year periods. Finally, the chronologies for plots H9 and H14 reflected moderate and sustained growth increases beginning approximately 35 years after plot initiation. The increases lasted about 10 years, with growth rates approximately 50% greater than the previous 10-year period.

Timing of understory reinitiation on each Huron plot is shown relative to the radial growth patterns in Fig. 4. On four of the plots (H2, H4, H6, H10), understory reinitiation and (or) continuous understory establishment began within a 5-year period subsequent to the radial growth decreases that occurred approximately 30–35 years (H2, H4, H10) or 40–45 years (H6) after plot initiation (Fig. 4). On plots H9 and H14, both understory reinitiation and continuous understory establishment started soon after the persistent radial growth increases that began 35 years

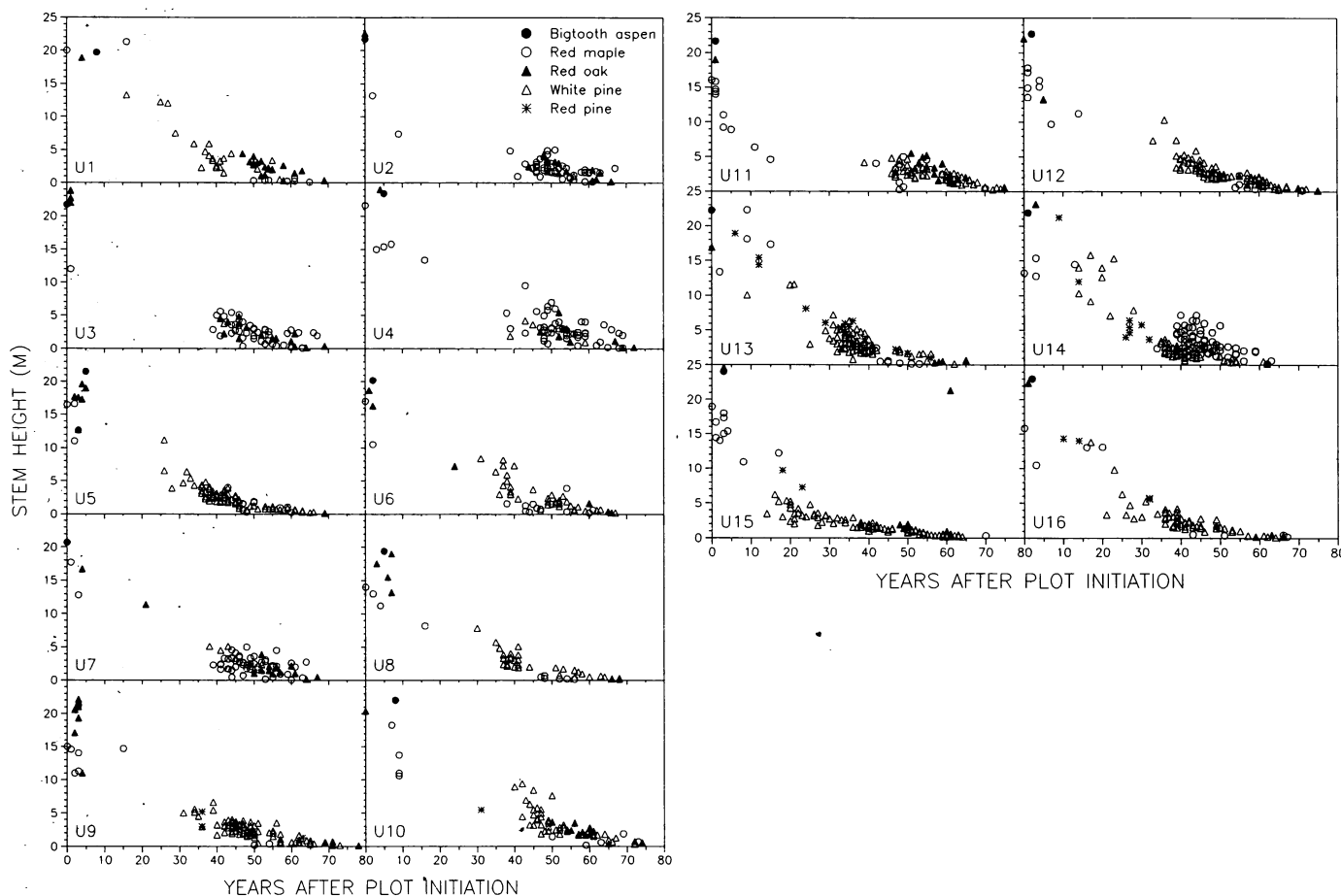


FIG. 2. Age-height distributions for all sampled stems on the 16 UMBS plots. Individuals ≥ 1.5 m tall were completely sampled on each plot. Individuals < 1.5 m tall were subsampled. Note that each plot contained an additional 15–35 bigtooth aspen ramets of similar age as the sampled stem. The red oak in the upper right corner of plot U15 was actually an individual from plot U16 that predated the remaining individuals on the plot by approximately 20 years.

after plot initiation. On the remaining plots, neither understory reinitiation nor continuous understory establishment began in association with any distinct feature of the radial growth chronologies. The shapes of the cumulative establishment distributions for advanced regeneration are worth examining because they represent the establishment patterns of individuals that are presumably most likely to recruit to dominant canopy positions. On most plots, the slopes of the establishment distributions for advanced regeneration were high initially, or they increased soon after the start of understory reinitiation.

A consistent feature of most UMBS chronologies was an increase in mean ring-width index beginning approximately 35–40 years after plot initiation (Fig. 5). At their maximum, growth rates during these increases averaged 83% above the previous 10 year period and persisted for at least 15 years. Radial growth rates prior to the increases were either consistently low for at least 10 years (plots U1–U2) or slowly increasing for 15–20 years (plots U5, U7–U8, U14, U16). Some of the chronologies show marked decreases in radial growth 15–20 years after plot initiation (plots U6, U8–U12, U16). The lack of this feature in other chronologies probably reflects actual growth patterns of the sampled trees (plots U1, U15), while in others it probably reflects the short lengths of the chronologies (plots U4, U13–U14).

In the UMBS plots, understory reinitiation was not associated consistently with any obvious feature of the ring-width chronologies (Fig. 5). In contrast, continuous understory establishment on most plots began concurrently with or soon after the radial growth rate increase that occurred 35–40 years after forest initiation (Fig. 5). An exception to this trend was plot U15. As noted previously, continuous understory establishment on this plot began 13 years after plot initiation. This did coincide, however, with the start of a large ring-width increase that persisted for over 15 years. Radial growth rate during this increase was 150% above the previous 2- to 3-year period (Fig. 5). Unfortunately, the ring-width chronology for this plot did not begin early enough to adequately assess growth patterns much before this increase. On most plots, large increases in the slopes of the cumulative establishment distributions for advanced regeneration often coincided with the start of continuous understory establishment and the concurrent increases in ring-width indices (Fig. 5).

White pine seed-source characteristics at UMBS

White pine was the dominant tree species regenerating on most of the UMBS plots (Fig. 2). Notable exceptions included plots U2–U4 and U7, which were dominated by red maple, and plot U14, which had large amounts of both white pine and red maple. On most plots, white pine was also the first

TABLE 2. Structural attributes of the Huron and UMBS plots

Plot	Huron						UMBS					
	Overstory ^a		Plot age (years)		Understory (stems/ha) ^d		Overstory ^a		Plot age (years)		Understory (stems/ha) ^d	
	m ² /ha	% aspen ^b	Mean ^c	Max.	≥1.5 m tall	0–1.5 m tall	m ² /ha	% aspen ^b	Mean ^c	Max.	≥1.5 m tall	0–1.5 m tall
1	54.3	83	66	70	735	128 785	21.6	75	71	75	716	79 187
2	44.8	72	67	70	74	46 887	30.3	88	69	72	1221	40 854
3	32.6	71	67	68	515	93 210	26.3	74	72	73	1010	35 833
4	40.9	93	64	65	2720	72 941	37.7	76	72	75	1116	54 188
5	32.1	53	66	69	478	37 941	27.0	63	71	74	1558	44 166
6	34.7	59	67	69	37	52 537	28.2	84	72	73	632	34 167
7	31.1	81	67	70	1838	56 703	17.7	87	71	73	1179	100 833
8	35.9	81	65	66	919	42 941	20.6	69	71	75	526	22 500
9	36.3	85	66	67	4154	66 666	32.7	62	76	79	1979	68 354
10	36.1	64	66	66	4411	90 833	29.5	89	75	82	1179	79 166
11	39.3	72	66	70	3272	46 666	25.7	74	81	83	1642	65 833
12	44.3	66	66	70	993	129 166	26.5	68	78	81	1726	159 166
13	46.5	80	65	67	662	107 499	30.8	78	67	71	2231	89 187
14	49.4	78	66	67	993	111 666	33.8	77	70	73	2968	99 166
15	38.3	60	65	68	0	175 833	29.4	65	71	74	1200	112 500
16	47.3	80	67	69	551	67 500	39.8	71	71	73	1326	58 333
17	65.0	80	66	68	257	66 274						
18	50.1	58	66	67	2316	104 534						
19	35.0	41	65	70	2757	87 107						
20	38.9	88	64	66	2794	48 995						

^a Stems >10 cm DBH.^b Relative basal area of bigtooth aspen.^c Mean age of all stems establishing within 10 years of plot initiation.^d Stems establishing subsequent to the start of understory reinitiation.

species to begin establishing in the forest understory, including plots U7 and U14. The remnant white pine seed trees provided an opportunity to examine the relationship between seed-source characteristics and the timing of understory reinitiation for this species.

Differences in white pine seed-source characteristics accounted for a large and significant proportion of variation in timing of understory establishment among plots ($r^2_{\text{adj}} = 0.82$; standard error of estimate (SEE) = 1.748; $P = 0.0004$). This analysis excluded plots U2 and U3, since by definition, initial understory reinitiation of white pine had not occurred on these plots. Differences in seed-source characteristics accounted for a low and only marginally significant proportion of variation in timing of continuous understory establishment among plots ($r^2_{\text{adj}} = 0.53$; SEE = 2.468; $P = 0.052$). Note that this analysis excluded not only plots U2 and U3, but also plots U4 and U7, since continuous understory establishment of white pine, by definition, had not yet occurred on these plots. The model for initial understory reinitiation was reanalyzed after excluding plots U4 and U7, as well as plots U2–U3. The results were marginally improved over the results that included plots U4 and U7 ($r^2_{\text{adj}} = 0.87$; SEE = 1.313; $P = 0.0008$).

The regression results suggest that timing of white pine understory reinitiation, and hence the length of time new stem establishment was prevented for this species, may have been influenced by remnant seed-source characteristics. Initial establishment was observed to occur earlier on plots in close proximity to several large seed trees, relative to plots with less-favourable seed-source characteristics. In contrast, the influence of remnant seed-source characteristics on the timing of continuous understory establishment of white pine

appeared to be much weaker, suggesting additional controls on this event.

Discussion

Many of the studies that have documented both the stem exclusion and understory reinitiation phases of even-aged forest development have either been based on results from one or few replicate plots (Oliver et al. 1985; Roberts and Richardson 1985; Abrams and Nowacki 1992) or have pooled data from replicate samples into a single forest-level analysis (Bloomberg 1950; Oliver et al. 1985; Harcombe 1986; Sharik et al. 1989; Segura and Snook 1992). These methodologies are inappropriate for assessing the variability and repeatability of developmental patterns within and among landscapes characterized by homogeneous site conditions and disturbance histories. Characterizing the repeatability of developmental patterns may be an important first step in identifying the mechanisms that control stem exclusion and understory reinitiation in various forest types. For example, Peet and Christensen (1987) argue that understory reinitiation in most even-aged forests is triggered by an increase in resource availability following density-independent mortality of mature overstory individuals late in even-aged development. In forests dominated by bigtooth aspen, complete overstory deterioration can progress rapidly (<10 years, Graham et al. 1963; Laidly 1990). If understory reinitiation in these forests is triggered by mortality of senescent canopy dominants, then it should begin synchronously across space and it should also occur late in even-aged development.

In the current study, the population age structures of surviving individuals on plots within the Huron landscape

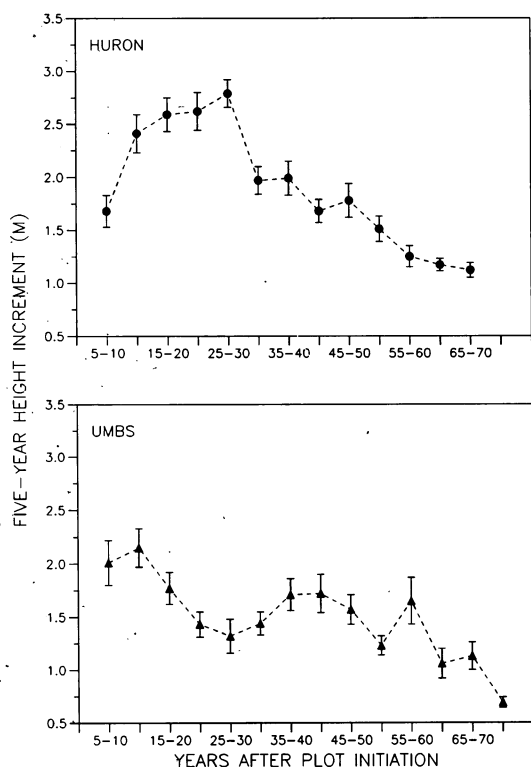


FIG. 3. Five-year height increment curves for the sampled bigtooth aspen in each forest. Means are shown with ± 1 SE. Sample size for the Huron forest is 20. Sample size for the UMBS forest is 16 (14 at 5–10 years).

reflected synchronous developmental patterns. An initial cohort of trees established within a 10-year period, and new establishment was curtailed for approximately 35 years, after which time individuals again began to establish in the forest understory. In contrast, the developmental patterns within the UMBS landscape were more variable. An initial cohort of trees established within a 10-year period, but the length of a stem exclusion period was highly variable (>0–35 years). Synchronous development was a characteristic of the UMBS forest only under a more restrictive definition of continuous understory establishment.

In both forests, understory reinitiation and increases in establishment frequency began when dominant bigtooth aspen were at most 67% of their total heights at maturity (and often much less) and no more than half of their maximum age in the Great Lakes region (Graham et al. 1963). The mechanism triggering understory reinitiation in these forests was not increased resource availability occurring in response to overstory deterioration late in even-aged development, despite synchronous developmental patterns in the Huron forest. The results do suggest that an increase in resource availability occurring relatively early in forest development may have influenced the timing of understory reinitiation, at least at UMBS.

We hypothesized that understory reinitiation would be associated with radial growth increases in surviving overstory stems, with both events occurring in response to increases in resource availability following natural thinning within the bigtooth aspen overstory. Results from the radial growth analyses provide only partial support for this hypothesis. On most

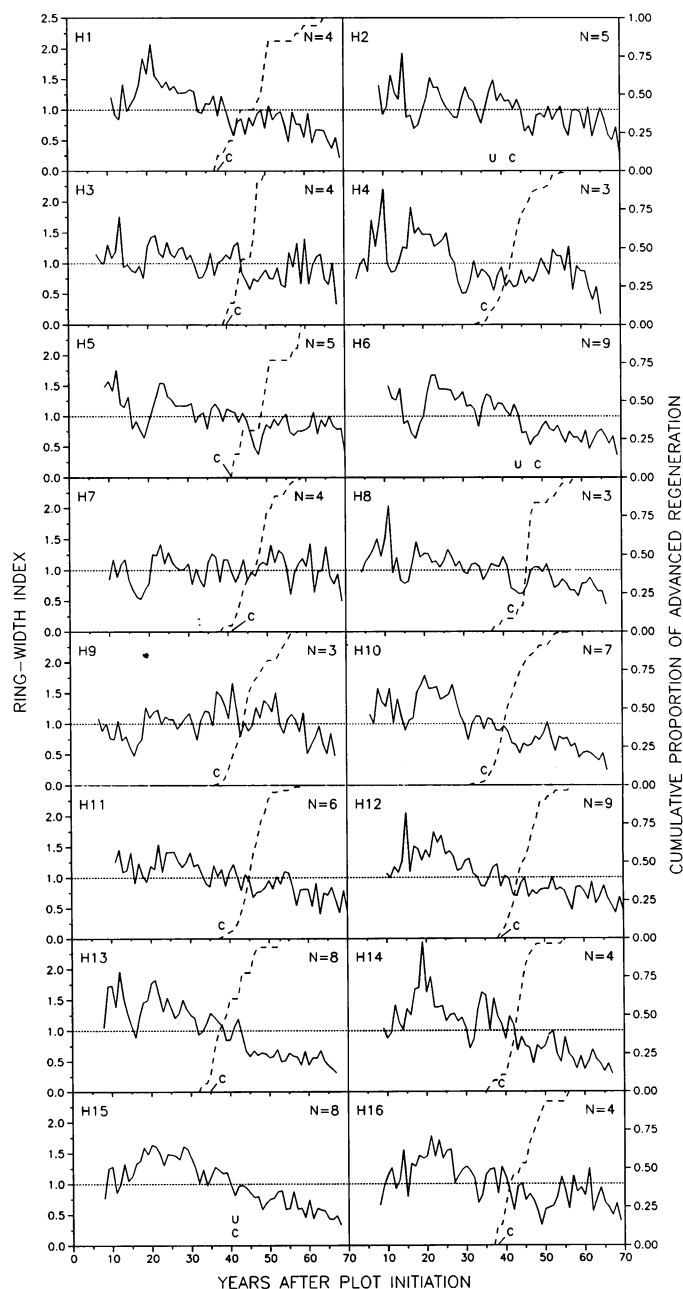


FIG. 4. Ring-width indices (solid lines) for the Huron plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The dotted line at a ring-width index of 1.0 is the standardized mean for the entire chronology (see text for derivation of ring-width indices). The broken line in each graph is the cumulative proportion of advanced regeneration (stems ≥ 1.5 m tall) establishing across time (scale is on the right side of each plot). The beginning of each cumulative establishment distribution marks the start of understory reinitiation (at least two stems establishing every 5 years for a minimum of 20 years; indicated by a U for plots without advanced regeneration). The C in each graph marks the start of continuous understory establishment (at least one stem establishing every year, or two every 2 years, for a minimum 10 years).

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UMBS plots, the bulk of new understory establishment typically began soon after large and persistent radial growth increases, which began 30–35 years after forest initiation. We cannot be certain that the increases occurred in response

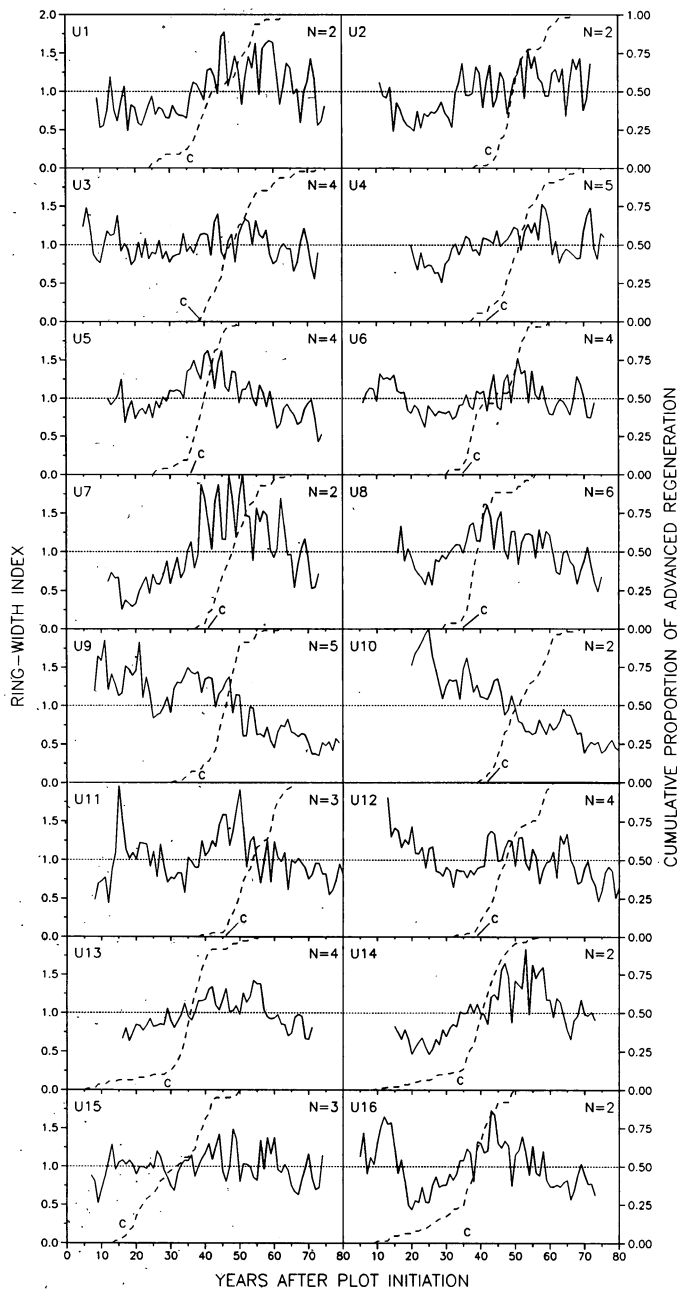


FIG. 5. Ring-width indices (solid lines) for the UMBS plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The dotted line at a ring-width index of 1.0 is the standardized mean for the entire chronology (see text for derivation of ring-width indices). The broken line in each graph is the cumulative proportion of advanced regeneration (stems ≥ 1.5 m tall) establishing across time (scale is on the right side of each plot). The beginning of each cumulative establishment distribution marks the start of understory reinitiation (at least two stems establishing every 5 years for a minimum of 20 years). The C in each graph marks the start of continuous understory establishment (at least one stem establishing every year, or two every 2 years, for a minimum 10 years).

to natural thinning. However, concentrated waves of density-dependent mortality, subsequent increases in resource availability, and growth releases of surviving stems are thought to be characteristic developmental features of most even-aged

forests (Oliver and Larson 1990), including those dominated by aspen (Graham et al. 1963, pp. 90–94). In the Huron forest, a persistent increase in radial growth rate, occurring in association with understory reinitiation, was a feature of only two of the 16 plots examined. On some of the remaining plots, understory reinitiation was associated with small to moderate radial growth changes; i.e., a short period of increased growth that followed a 2- to 3-year period of reduced growth. Such small and short-lived radial growth changes are generally believed to result from exogenous factors influencing tree growth, for example climatic fluctuations or insect defoliation, rather than changes in resource availability associated with stand dynamics (Lorimer 1985). However, Graham et al. (1963) reported that growth reductions associated with natural thinning waves in aspen were of short duration and that subsequent growth increases within the aspen overstory were of lesser magnitude and shorter duration than those that typically occur following a major canopy opening disturbance (for examples of the latter see Lorimer 1980, 1983, 1985). Such subtle changes in overstory growth rates in response to natural thinning would be difficult to distinguish from those caused by exogenous factors.

If the majority of new understory establishment did occur in response to increased resource availability following mortality of suppressed stems then, by default, crown or root growth of the remaining overstory individuals must have been inadequate to sequester all available resources. The combined influence of natural thinning and a reduced rate of crown expansion in surviving stems has been hypothesized to result in canopy closure that is reached asymptotically early in the course of even-aged stand development and decreases thereafter (Zeide 1987, 1991). The height increment patterns for the few sampled bigtooth aspen ramets did suggest that crown expansion rates may have been low at times that coincided with understory reinitiation (Fig. 3). In the Huron forest, height increment dropped substantially just prior to understory reinitiation. At UMBS, bigtooth aspen height increment actually increased slightly at a time coincident with continuous understory establishment; however, overall height growth rates were always low in this forest, except for early in forest development. Changes in rates of root growth may be a particularly important factor influencing understory establishment in aspen-dominated forests, given the taxon's ability to saturate soil space rapidly following fire through growth of clonal root systems (Stoeckeler and Macon 1956; Zahner and Crawford 1965; Barnes 1966; Graham et al. 1963). Limited research suggests that a clone's inter-ramet root system deteriorates progressively during forest development, with most ramets having independent root systems by an early age (e.g., 32 years, Ruark and Bockheim 1987). This gradual deterioration, either combined with or in response to self-thinning, may push soil resource availability above some minimum threshold required for a new establishment in the forest understory.

In the current study, patterns of white pine establishment at UMBS suggest that variation in seed availability early in forest development may have also influenced the timing of new understory establishment. On some UMBS plots, initial establishment of white pine occurred soon after radial growth increases in the overstory, while on other plots initial establishment began prior to any obvious radial growth increase. The variation in timing of initial white pine establishment was

significantly related to remnant seed-source characteristics. Initial establishment occurred earlier on plots in close proximity to several large remnant white pine seed trees, sometimes prior to any radial growth increase. This relationship suggests that the timing of white pine understory reinitiation may have depended on the maturation or proximity of a local seed source. A similar argument has been used to account for differences in initial establishment times of white pine in other bigtooth aspen-dominated forests at UMBS (Sharik et al. 1989). However, in the current study, there was a correspondence between large increases in the frequency of white pine establishment, subsequent to understory reinitiation, and increases in radial growth rates of overstory red maple and red oak. Additionally, the relationship between timing of continuous white pine establishment and remnant seed-source characteristics was weak.

These results suggest that timing of new establishment of white pine may have been influenced by an interaction between changing resource levels in the forest understory and seed availability. Limited early establishment of white pine occurred on plots that received substantial seed input from remnant trees during early forest development; however, the bulk of new establishment may not have occurred until resource levels in the forest understory became favorable for survival. An alternative explanation for the establishment patterns of white pine is that increases in resource availability actually hastened the reproductive maturation of seed trees that had either established immediately following disturbance or survived as advanced regeneration from the predisturbance forest. A near-synchronous seed-source maturation, acting alone or in combination with improved resource levels in the forest understory, could have led to the large increases in white pine establishment frequency that occurred on most plots.

The establishment patterns on plots with hardwood-dominated understories (predominantly red maple) also suggest seed-source maturation may have influenced the timing of understory reinitiation. In both forests, the stem exclusion periods for red maple lasted 30–40 years. A delay in new red maple establishment in aspen-dominated forests has been attributed to low seed availability prior to reproductive maturation of a post-disturbance cohort of sprout-origin trees (Roberts and Richardson 1985; Sakai et al. 1985; Sakai 1990). Observations on mature red maple (and red oak) in the Huron forest (Palik and Pregitzer 1992a, 1992b) and at UMBS (Roberts and Richardson 1985; Sakai et al. 1985; Scheiner et al. 1988; Palik and Pregitzer 1992a) do indicate that many overstory individuals were of sprout origin. Presumably, if a mature red maple seed source had existed early in the development of the UMBS forest, some individuals of this relatively understory tolerant species (Walters and Yawney 1990) would have established at least as early as less-tolerant white pine (Wendel and Smith 1990). While understory reinitiation on plots with red maple dominated understories may have been dependent on maturation of local seed sources, new understory establishment of this species sometimes began following a radial growth increase in the overstory. As with white pine at UMBS, the correspondence between new understory establishment of red maple and radial growth increases in the overstory suggests that increases in resource availability may have led to increased establishment of new stems. Reproductive maturation of red maple seed sources and

the increases in resource availability that led to new establishment may have occurred at similar times simply by chance, or again, it is possible that increases in resource availability actually hastened the maturation of local seed sources.

Summary and conclusions

Quantification of variability and repeatability in forest development patterns is an essential first step to developing a comprehensive mechanistic understanding of stem exclusion and understory reinitiation in even-aged forests. The current study provides this first step for a forest type that has been under-studied from a stand development perspective. The results from the Huron and UMBS landscapes indicate that bigtooth aspen dominated forests do follow a pattern of development thought to be characteristic of many forests that initiate following major disturbance (Oliver 1981; Peet 1981; Peet and Christensen 1987). Rapid initial cohort establishment, stem exclusion, and understory reinitiation were repeatable features of the age distributions of these forests, both within and between landscapes. While the bulk of regeneration in the forest understory began to establish at near synchronous times within each forest, there was some variation in the timing of early understory reinitiation at UMBS. The sampling scheme used allowed this variation to be detected. For example, if research at UMBS had been restricted to the one stand containing plots U13–U16, there would have been little reason to believe that a true stem exclusion period was a characteristic feature of bigtooth aspen forest development. The results also indicate that understory reinitiation was not triggered by mortality of dominant overstory stems late in even-aged development. The timing of understory reinitiation may have been influenced by an interaction between increased resource availability, possibly in response to natural thinning, and availability of local seed sources. The factors controlling stem exclusion and understory reinitiation may be even more complex than recent overviews of forest development suggest (Oliver and Larson 1990; Peet and Christensen 1987), since these treatments have largely ignored the potential influence of seed source on new establishment. Our results suggests that there is still more to be learned about even-aged forest development, particularly with respect to the mechanisms that control stem exclusion and understory reinitiation. The results of this study will prove useful for designing the experimental studies that are needed to identify these mechanisms.

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